TAXONOMIC AND BIOLOGICAL STUDIES OF *DIVERSINERVUS CERVANTESI* (GIRAULT) (HYMENOPTERA : ENCYRTIDAE), A PRIMARY PARASITE OF SOFT SCALE INSECTS

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Abstract

Diversinervus cervantesi (Girault) (Hymenoptera: Encyrtidae) is a primary, gregarious endoparasite of soft and wax scale insects (Homoptera: Coccidae), recorded from Australia, Malaysia and Israel. The species is deuterotokous, with brachypterous females and rare macropterous males. The adult female, the hitherto undescribed male and the developmental stages are described and figured.

The eggs of *D. cervantesi* are laid into the hind gut of the host. Development takes 21 days at 28°C, 28 days at 24°C, 44 days at 20°C; the threshold of development is 12.5°C and the thermal constant is 327.8 day-degrees. The females exhibit high longevity (average 45 days at 26°C) and high fecundity (average 187 progeny). They are very sensitive to low relative humidity, whereas temperatures in the range of 24 - 32°C to not have a pronounced effect on their longevity.

Two informal species groups are proposed for the 10 valid species presently included in the genus *Diversinervus* Silvestri: The **elegans group**, comprising *desantisi* Compere, *elegans* Silvestri, *madgaoensis* Hayat, Alam and Agarwal, *paradisicus* (Motschulsky), *scutatus* Compere, *silvestrii* Waterston and *stramineus* Compere, in which the females have tufts of bristles on both the mesoscutum and scutellum, the head of the males is metallic, the eggs are banded and the first-instar larvae have open tracheal systems; and the **smithi group**, comprising *cervantesi* (Girault), *masakaensis* Compere and *smithi* Compere, in which the females lack the mesoscutar tuft, the head of the males is yellow, the eggs are unbanded and the first-instar larvae have closed tracheal systems.

A revised key to the species of *Diversinervus* is presented.

INTRODUCTION

Diversinervus cervantesi (Girault) (Hymenoptera: Encyrtidae) is a primary gregarious endoparasite of various soft and wax scale insects (Homoptera: Coccidae). It is an unusual species, with brachypterous females and rare macropterous males which, in spite of its limited mobility, appears to be rather widespread, having been recorded so far from Australia, Malaysia and Israel. Inasmuch as it was discovered in Israel for the first time only a few years ago, we assume that it may have invaded the country fairly recently, presumably with host material. The taxonomic and biological studies reported herein were conducted as part of a long-term research project on the hymenopterous parasite fauna of Israel.

The genus *Diversinervus* Silvestri is closely related to *Cheiloneurus* Westwood, a genus of injurious hyperparasites, and was therefore at first also thought to be hyperparasitic. However, Compere (1931) has shown that the type-species, *D. elegans* Silvestri, in fact develops as a primary parasite of coccids. All known members of the genus are presently believed to be primary parasites, and some of them have been utilized in the biological control of coccid pests (Bartlett 1978).

Diversinervus was initially separated from *Cheiloneurus* by having conspicuous tufts of bristles on both the mesoscutum and scutellum of the female. This, however, proved to be an unreliable generic character. Several bona fide members of *Diversinervus*, including *cervantesi*, resemble *Cheiloneurus* in lacking the mesoscutas tuft (Fig. 1). As pointed out by Compere (1940), the main diagnostic character by which *Diversinervus* may be distinguished from *Cheiloneurus* and other related genera is the peculiar structure of the female head, with the frontovertex expanded into a frontal ledge and the face meeting it in a sharp angle (Fig. 1). Also, in most species of *Diversinervus*, the marginal vein of the female fore wing is relatively short, subequal in length to the stigmal vein, whereas in *Cheiloneurus* it is considerably longer.

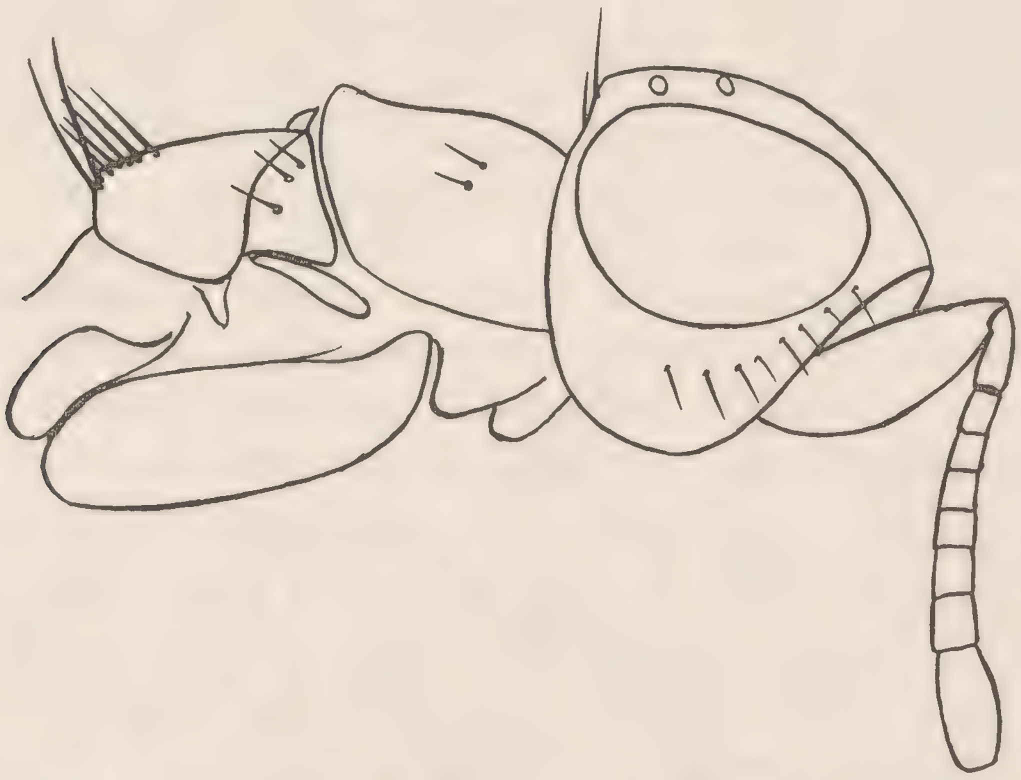


Fig. 1. **Diversinervus smithi** Compere, Female head and thorax
(From Compere, 1940)

Diversinervus cervantesi (Girault), n. comb.

Cheiloneurus cervantesi Girault, 1933. Some Beauties Inhabitant Not of Commercial Boudoirs but of Nature's Bosom, Notably New Insects. Priv. Publ., Brisbane, p. 4.

Girault (1933) described this species as follows:

"*Cheiloneurus cervantesi*. Subapterous, wing 1 fuscous at apex. Like *Diversinervus* genotype but ocelli absent(?), hind margin pronotum with thick black bristles like those of hair-tuft, thicker mesad; metatarsus white. Discal cilia absent, no stigmal or postmarginal vein. Ex *Pulvinaria*. Nambour, Feb. A. R. Brimblecombe."

REDISCRIPTION

Female (Figs. 2-20): Head in lateral view (Fig. 2), triangular; in dorsal view (Fig. 3), somewhat wider than the thorax (1.0 - 1.1), somewhat wider than long (1.10 - 1.25); frontovertex deeply emarginate posteriorly, mostly parallelsided, 3.5 - 3.9 times as long as wide, 0.22 - 0.26 width of head, smooth, bearing 2 longitudinal rows of fine setae, with 2 pairs of longer, coarser, black setae along occipital margin, on either side of indentation. Ocelli small, in an equilateral triangle, the posterior pair about twice their own diameter from orbits, 5 diameters from occipital margin. Eyes large, 1.4 - 1.6 times as long as wide, bordered by a row of fine setae and bearing short, sparse interommatidial setae. Face and cheeks reticulate; toruli (Fig. 11) subtriangular, their bases at about one-third the distance between clypeal and frontal margins; scrobes meeting anteriorly. Mouthparts (Figs. 4-6): Mandibles tridentate, 2.0 - 2.5 times as long as wide, bearing about 7 setae, the denticles subequal. Maxillary palpi 4-segmented, the distal segment about twice as long as the penultimate (1.85 - 2.20), bearing several subapical setae, the longest somewhat longer than the segment itself. Labial palpi 3-segmented, second segment the shortest and wider than long, the distal one bearing several setae.

Antennae (Figs. 7-11): Radicle stout, longer than wide, bearing several finger-like sensilla. Scape moderately expanded antero-ventrally, about 2.7 times as long as wide, 2.4-2.8 times longer than the pedicel, 1.10-1.25 times longer than the club. Pedicel conical, about twice as long as wide (1.8 - 2.3), about twice longer and one-fifth to one-third wider than the first segment of the funicle. Funicular segments I-III as long wide or somewhat longer, segments IV-VI as long as wide; segments I-IV subequal in length, V about one-third longer (1.23 - 1.43) and one-fourth wider (1.20 - 1.35) than IV, VI somewhat larger than V; setae on segments I - III about as long as the segments. Club about 3 times as long as wide (2.6 - 3.3), equal in length to the preceding 4 segments and one-third to one-half of segment II combined, about one-fifth wider than segment VI (1.08 - 1.32); all 3 club segments bearing longitudinal sensilla, funicle V and VI bearing one sensillum.

Thorax (Figs. 2, 12-13): As in many other brachypterous encyrtids, apears rather undeveloped, widening posteriorly, with small mesonotal and metanotal sclerites and relatively large pronotum, tegulae and mesopleura. Pronotum large, somewhat wider than long, widening posteriorly, overlapping the anterior margin of mesoscutum, reticulate, bearing 3 transverse rows of about 20 setae each, those of the posterior row black, longer and coarser submedially. Mesoscutum convex, as long as the pronotum and somewhat longer than wide, mostly reticulate-strigose, lacking a tuft of bristles but with a smooth area latero-posteriorly bearing one lateral row and 3 irregular posterior rows of silvery setae. Axillae meeting mesally, reticulate, each bearing 1-2 pale setae. Scutellum convex, rather narrow, as long as the mesonotum and one-fourth to one-third longer than wide, occupying only one-third to two-fifths width of thorax (0.34 - 0.40), reticulate, bearing a dense tuft composed of 2 submedian longitudinal rows of 4-6 black, coarse bristles each, surrounded by several shorter setae, and a pair of longer erect subapical bristles. Tegulae large, triangular, reticulate, each bearing 4 setae. Mesopleura large, convex, smooth, readily visible in dorsal view. Metanotum transverse, somewhat arcuate, 4-5 times as wide as long, with coarse oblique striation. Propodeum (Fig. 12) almost as wide as the thorax, about 3 times as wide as long, mostly smooth, with deep transverse furrows along anterior and posterior margins and some coarse striation antero-laterad of spiracles, the latter areas bearing a single fine seta.

Gaster (Figs. 2, 14 - 15) about one and one-half times as long as wide, somewhat shorter than the thorax and about as wide; first tergite ring-like, the second (= abdominal tergite III) large, reticulate, bearing what appear to be numerous discoid sensilla; subsequent tergites reticulate, bearing sparse setae; epipygium large, smooth, bearing sparse setae. Cerci situated at basal one-third of gaster, bearing 3 long setae and 2 short setae. Ovipositor about 0.8 - 0.9 length of gaster, slightly exserted, the hypopygium covering only its basal one-third or so.

Legs (Figs. 2, 16, 17) well developed. Mid-tibial spur somewhat (up to 1.14 times) longer than the corresponding basitarsus.

Wings (Figs. 12 - 13, 18 - 20) greatly reduced, variable. Fore wing about as long as width of thorax, usually not reaching beyond second gastral tergite, narrow, about 6.5 times as long as wide (6.3 - 6.8); submarginal vein bearing 3-4 fine setae proximally, somewhat expanded distally and bearing 6-8 setae, usually reaching margin at apex of wing, with an apical bristle about as long as width of wing; a few fine discal setae along anterior margin and at postero-distal corner, marginal fringe usually absent; sometimes the wing is somewhat expanded beyond venation (Fig. 19), the distal area bearing discal setae and a short marginal fringe. Hind wing usually very narrow, considerably shorter than the fore wing, the vein reaching apex of wing, with 3 apical hamuli; occasionally (Fig. 20), the wing is larger, expanded beyond venation, bearing numerous discal and some marginal setae.

General coloration orange-yellow. Eyes dark purple, ocelli reddish brown. An arcuate dark brown stripe on face and cheeks, at level of antennal toruli. Distal one-third of mandible dark brown. Antenna concolorous with body, ventral margin of scape and dorsal margins of pedicel and funicle segments I-V lined with dark brown; first club segment suffused with brownish distally, second and third segments dark brown. Mesoscutum with a light metallic cross-band on posterior one-third, bearing silvery setae; scutellum somewhat paler yellow, with a pair of brown blotches posteriorly, on either side of tuft; propleura, prosternum and mesosternum lined with dark brown. Propodeum with brown blotches at postero-lateral corners. Gaster lined with dark brown on margins, with a semi-circular transverse dark brown blotch centrally, between cerci; cercal plates dark brown. Legs concolorous with body, the following parts translucent white: fore and hind coxae, all trochanters, basal two-thirds of fore femur, three-fourths of middle femur and one-third of hind femur, base of middle and hind tibia, and most of hind tarsus; dark brown on middle coxa, a spot near base of middle and hind tibia, and all pretarsi. Fore wing hyaline, marked with dark brown on proximal part of vein, on frenal fold at proximal part of posterior margin, and at apex, including distal part of vein; when somewhat expanded beyond venation, that apical part is hyaline, the dark brown area then forming an oblique cross-band from apex of vein to posterior margin. Hind wing hyaline.

Length: 1.20 - 1.56 mm.

Male (Figs. 21 - 27): Differing markedly from the female in the structure of head, antennae, thorax and wings, as well as in general coloration.

Head in lateral view, lenticular; in dorsal view, nearly as wide as the thorax (0.83 - 0.95), almost 3 times as wide as long (2.6 - 2.8), delicately reticulate; frontovertex broad, about one-third wider than long, about half width of head (0.47 - 51). Ocelli large, in an obtuse triangle (100°), the posterior pair about their own diameter from orbits, half a diameter from occipital margin. Eyes smaller than in the female. Toruli situated at about middle of face; scrobes meeting anteriorly. Mouthparts as in the female.

Antennae (Fig. 21) filiform. Radicle stout, 1.3 - 1.6 times as long as wide. Scape about 3 times as long as wide, distinctly shorter than the club. Pedicel about one and one-half times as long as wide (1.40 - 1.56), considerably shorter than the first segment of the funicle (0.5 - 0.7). All funicular segments elongate, subequal in width, bearing whorls of long setae, segments V - VI bearing several longitudinal sensilla; segments II-V subequal in length, about 3 times as long as wide, I and VI somewhat shorter, about 2.5 times as long as wide. Club undivided, elongate, 4 - 5 times as long as wide, about three-fourths longer and somewhat wider than the preceding segment, bearing long setae and several longitudinal sensilla.

Thorax (Fig. 22) well developed, convex, rather uniformly reticulate dorsally, the scutellum reticulate-strigose mesally. Pronotum conical, bearing 2 - 3 transverse rows of setae. Mesoscutum rather broad, somewhat wider than long, bearing numerous sparse setae. Axillae separate, their apices not meeting mesally, each bearing 1 - 2 setae. Scutellum triangular, somewhat shorter than the mesoscutum and about as long as wide, occupying one-half to two-thirds width of thorax (0.56 - 0.65), bearing 2 sparse, longitudinal rows of 6 - 7 setae each, the posterior pair longer than the rest. Tegulae triangular, smaller than in the female, each bearing several setae. Mesopleura large, smooth, not visible in dorsal view. Metanotum V-shaped, about 5 - 7 times as wide as long, with coarse oblique striation. Propodeum (Fig. 22) about as wide as the thorax, 3 - 4 times as wide as long, mostly smooth, with some transverse striation along anterior and posterior margins and antero-laterad of spiracles.

Gaster (Fig. 23) trapezoidal, about one and one-half times as long as wide, about three-fourths length of thorax (0.66 - 0.81) and about as wide, largely smooth, bearing sparse setae. Cerci as in the female. Genitalia (Figs. 23, 24) 3.4 - 5.5 times as long as wide, about two-fifths length of gaster (0.35 - 0.46), three-fifths to three-fourths length of middle tibia (0.58 - 0.76), exserted to about one-third length; digital sclerites about one-fifth the combined length of aedeagus and slender apodemes (0.17 - 0.23), bearing a single strong claw.

Legs (Fig. 25) similar to those of female. Mid-tibial spur about half as long as the corresponding basitarsus.

Wings (Figs. 26, 27) well developed. Fore wing about as long as the entire body, 2.5 times as long as wide (2.3 - 2.9), rather uniformly setose distad of speculum, the setae proximad of speculum somewhat longer and sparser; marginal fringe not exceeding one-tenth width of disc; submarginal veing somewhat widened on distal one-third, bearing 10 - 12 setae and numerous bullae; marginal vein twice as long as wide, subequal in length to the stigmal and postmarginal veins, bearing several setae; stigmal vein about one and one-half times as long as wide, widening distally, bearing 3 discal sensilla in a row at apex; postmarginal vein tapering toward apex, bearing several setae. Hind wing about 4-5 times as long as wide, two-thirds length of fore wing, uniformly setose except at base; marginal fringe not exceeding one-third width of disc; venation reaching to about two-thirds length of wing, the marginal vein bearing 3 apical hamuli.

Coloration considerably darker than in the female. Head orange-yellow, with a pair of small dark brown blotches on occiput, on either side of foramen. Eyes and ocelli purplish black. Antennae uniformly brown, scape somewhat paler, pedicel marked with blackish dorso-basally, flagellar setae dark brown. Pronotum dark metallic centrally, orange-yellow laterally; mesonotal sclerites dark metallic, with green reflections, sides of mesoscutum orange-yellow, lateral and posterior margins of axillae narrowly lined with orange-yellow; tegulae brownish, mesopleura brown; metanotum brown; venter of thorax orange-yellow. Propodeum mostly brown, the antero-lateral corners orange-yellow. Gaster entirely black. Legs mostly pale yellow; hind tibia faintly marked with brownish, fore tarsus brown, distal segment of middle and hind tarsi brownish. Wings hyaline, the venation blackish; submarginal vein of fore wing interrupted subapically by a short hyaline portion.

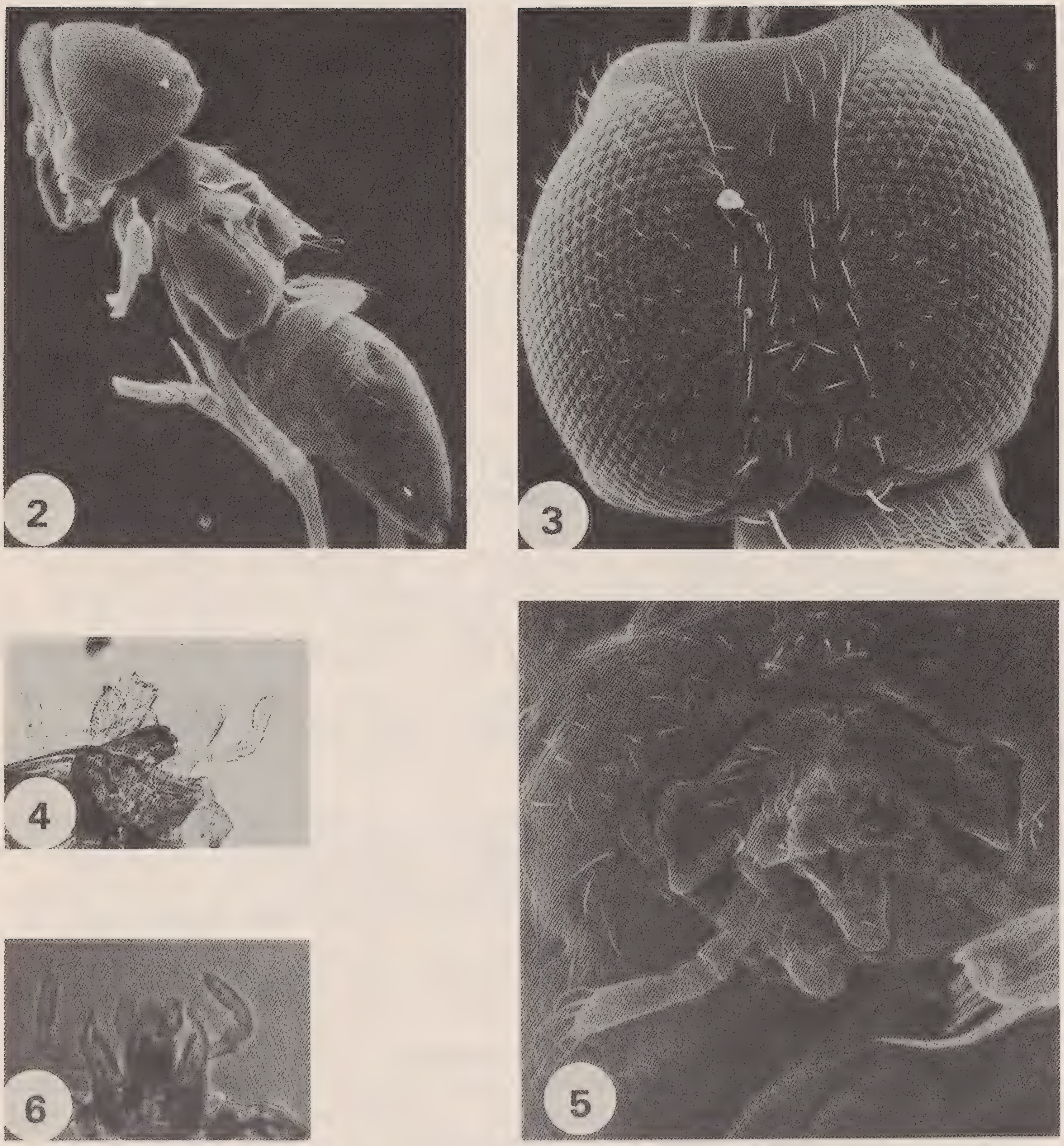
Length: 0.8 - 1.0 mm.

Redescribed from numerous male and female specimens, insectary-reared on *Coccus hesperidum* L. on citron melon, *Citrullus vulgaris* var. *citoides*, Rehovot. The stock had originated from 3 females, reared ex *Pulvinaria mesembryanthemi* (Vallot) on *Mesembryanthemum edule*, Rehovot, Israel.

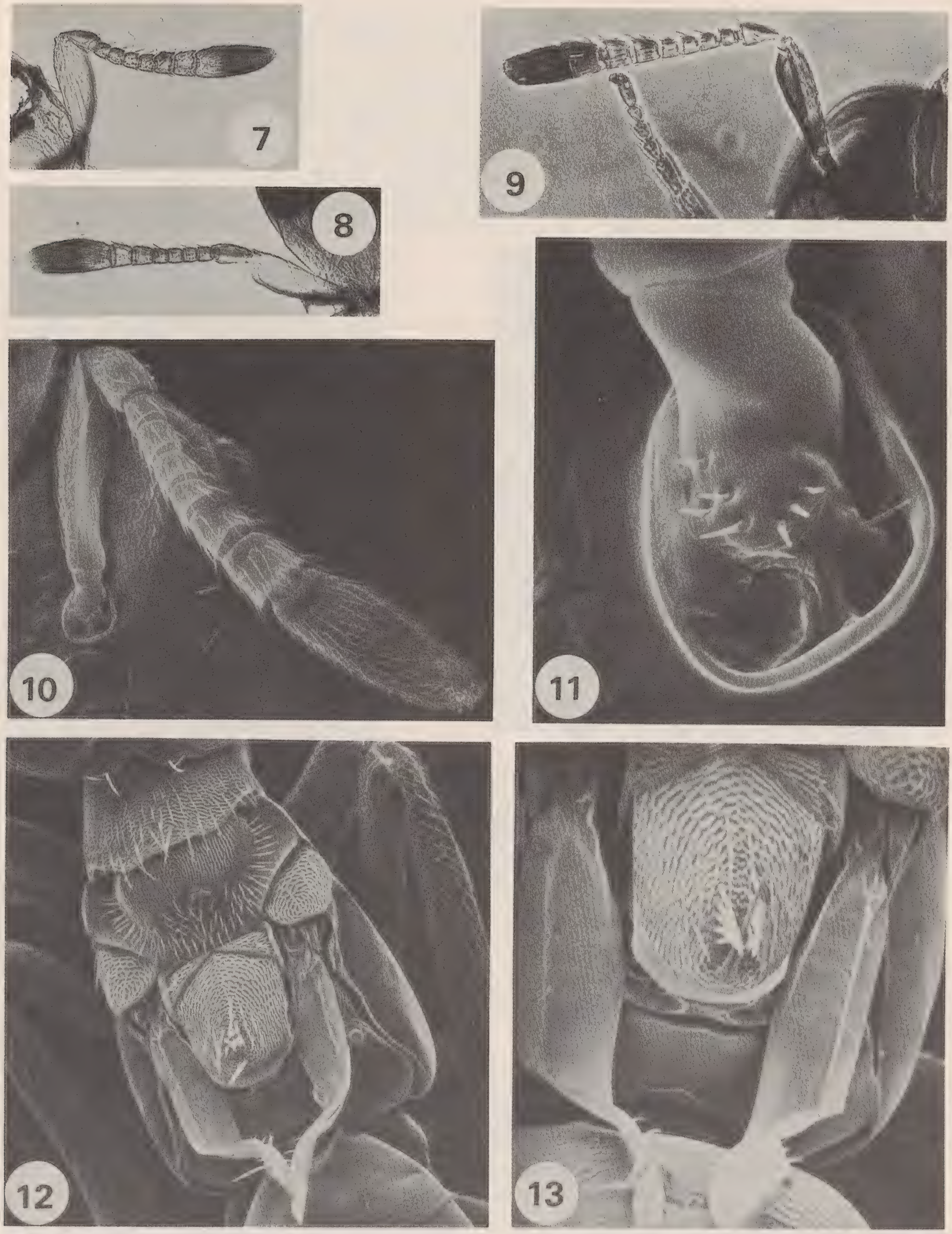
Notes: The type series of *cervantesi* was received on loan from the Queensland Museum, Brisbane, Australia. It consists of 2 female syntypes, mounted in balsam on one slide, labeled "Cheiloneurus cervantesi Gir. F Types" in A. A. Girault's handwriting. The body of one female lies under one cover glass, a head and the dissected parts of another female under another cover glass. We assume that the undissected head belongs to the undissected body, but this is by no means certain. Designation of a lectotype is therefore undesirable.

The Israel material described herein appears to be conspecific with the syntypes. Some of the syntype antennae seem to be somewhat more extensively pigmented, with the first club segment mostly - or entirely - fuscous, but antennal pigmentation appears to be variable in the type series (Figs. 7, 8) and cannot be used as a diagnostic character. Specimens received for identification from Malaysia (recorded as *Diversinervus* sp. by Chua, 1976) were also found to be conspecific.

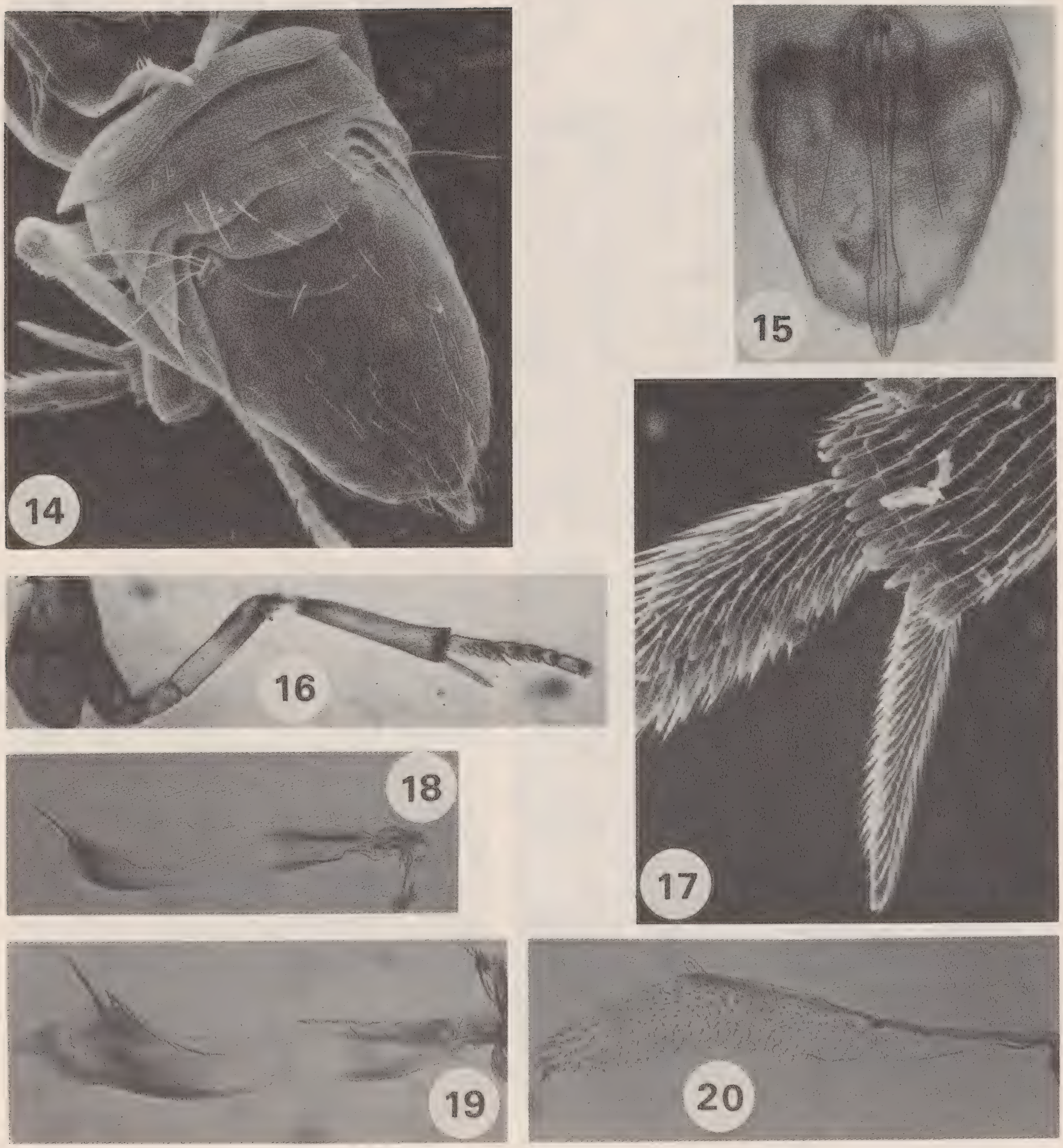
Although Girault (1933) compared *cervantesi* to the generotype of *Diversinervus*, he referred this peculiar species to the genus *Cheiloneurus* but failed to state his reasons for doing so. His decision was probably based on the absence of a mesoscutar tuft. This species is a bona fide member of the genus *Diversinervus*. It appears to be closely related to *D. smithi* Compere, a macropterous species described by Compere (1940) from South Africa. It resembles *smithi* in most aspects of structure, chaetotaxis, sculpture and coloration, differing mainly in the reduced wings and thoracic tergites of the female. Although Girault's tentative reference to the absence of ocelli in *cervantesi* was erroneous, the ocelli of the female are indeed



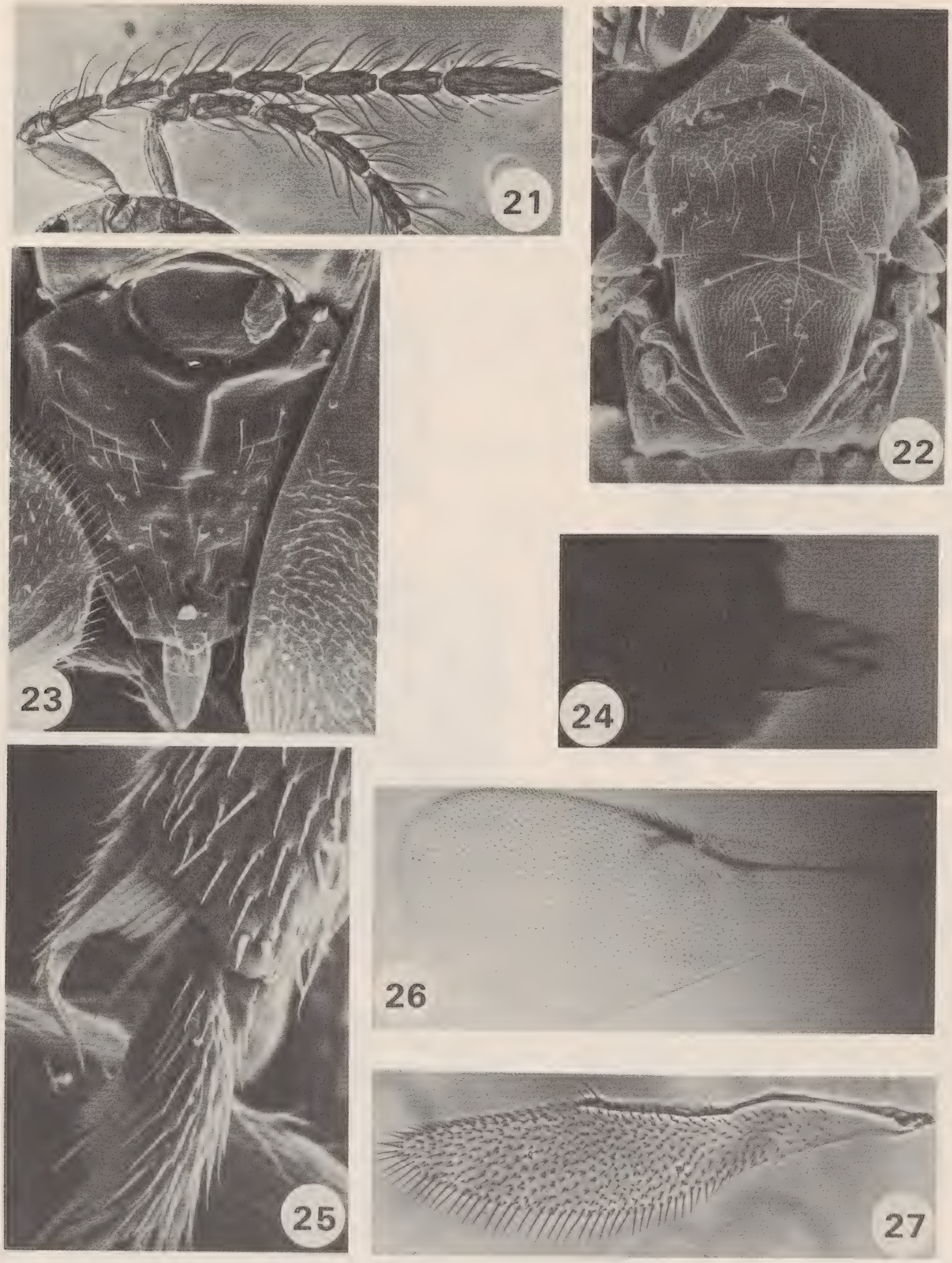
Figs. 2-6. **Diversinervus cervantesi** (Girault), female: 2, Lateral view of entire specimen (SEM). 3, Head, dorsal view (SEM). 4-6. Mouthparts (4 = syntype; 5 = SEM).



Figs. 7–13. **Diversinervus cervantesi** (Girault), female: 7–10, Antennae (7, 8 = syntype; 10 SEM). 11, Base of antenna (SEM). 12, Thorax, propodeum and fore wings (SEM). 13, Scutellum, axillae and fore wings (SEM).



Figs. 14–20. **Diversinervus cervantesi**(Girault),female: 14,15, Gaster (14 = SEM). 16, Middle leg. 17, Mid tibial spur and basitarsus (SEM). 18–19, Fore wings. 20, Hind wing, unusually developed.



Figs. 21–27. **Diversinervus cervantesi** (Girault), male: 21, Antennae. 22, Thorax and propodeum (SEM). 23, Gaster (SEM). 24, Genitalia. 25, Strigil of fore leg (SEM). 16, Fore wing. 27, Hind wing.

smaller and less conspicuous than those of *smithi*, and the posterior pair is situated somewhat farther from the occipital margin than in that species. Also, funicular segment V islined with blackish in *cervantesi*, entirely yellow in *smithi*; the middle coxa is brown in *cervantesi*, white in *smithi*; and the pronotal setae appear finer, less conspicuous, in the female of *smithi*. The two species are almost indistinguishable in the male sex. The males of *smithi* appear somewhat more extensively pigmented than those of *cervantesi*, the mesoscutum with less clearly defined yellow areas laterally and with strong violaceous reflections on the posterior half. The frontovertex appears somewhat narrower in the male of *smithi*.

As shown below, *D. cervantesi* also differs from *D. smithi* in the site of oviposition in the host, and in the morphology of the first-instar larva. The two species also appear to differ in their mode of reproduction: *D. cervantesi* is uniparental, whereas *D. smithi* is presumably biparental (Flanders 1939).

DEVELOPMENTAL STAGES

Egg (Figs. 28-31): The egg of *D. cervantesi* is unbanded (Maple 1947), similar to that of *D. smithi* (Flanders 1952). The ovarian egg (Fig. 28) is elongate, the dorsal aspect concave, with a narrow bulb, shorter than the egg proper and separated from it by a short, indistinct stalk.

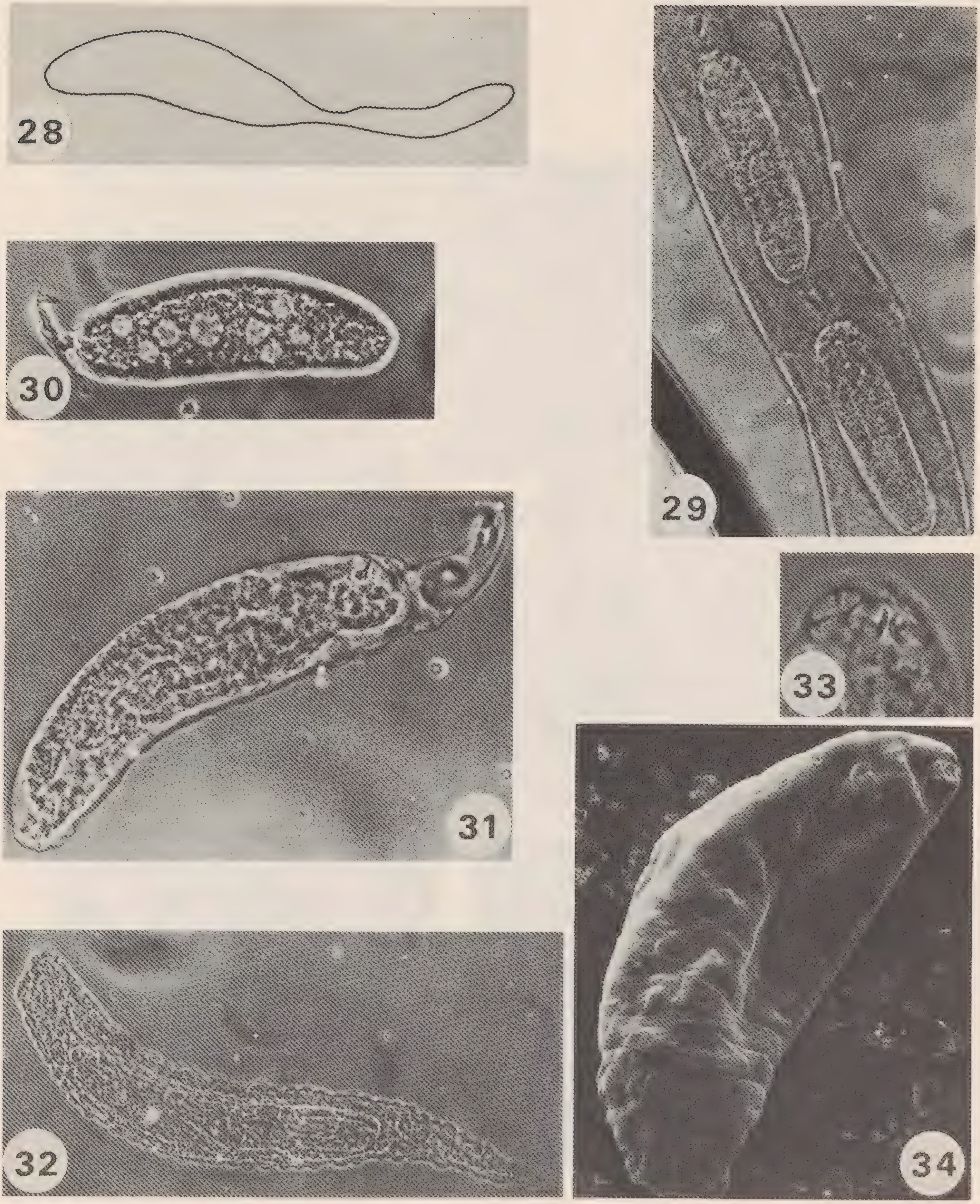
Unlike *D. smithi*, which reportedly oviposits in the suboesophageal ganglion of its host (Flanders 1952), *D. cervantesi* lays its eggs in the host's hind gut (Fig. 29). The deposited egg is banana-shaped, with the short, collapsed remnants of the bulb and stalk at its anterior end (Figs. 30, 31). It lies freely in the gut and does not change much in size after deposition. At 28°C, the mandibles and midgut of the developing embryo become evident on the fourth day after deposition (Fig. 31).

Larva (Figs. 32-40): The first-instar larva (Figs. 32, 33) leaves the hind gut soon after hatching. Unattached to the egg chorion, it floats freely in the body fluids of the host. It is orange-yellow, distinctly caudate, and lacks the cephalic vesicles reported in *D. smithi* (Flanders 1952). Like other encyrtids with unbanded eggs, the first-instar larva of *D. cervantesi* has a closed tracheal system (Maple 1947). The average size of this instar increases during its development, from 333 x 57 to 600 x 105 μ. The mandibles (Fig. 33) are sickle-shaped, 8.5 μ long, with a bifid base.

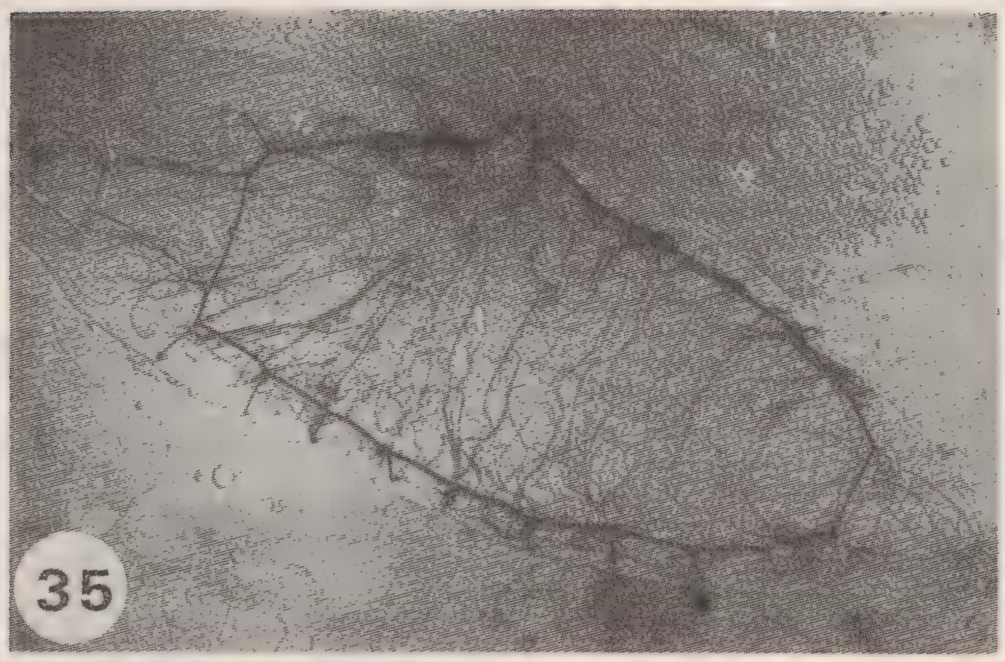
The fully-developed larva (Figs. 34-40) is brown-yellow, hymenopteriform, about 1.5 mm long. It has an open, peripneustic tracheal system, with 9 pairs of functional spiracles present in thoracic segments II, III and abdominal segments I-VII (Figs. 35, 36). Cephalic skeleton as in Figure 37 (terminology adapted from Vance and Smith, 1933). The mandibles (Figs. 37-39) are 45 μ long, with a strong, straight tooth and a subquadrate base.

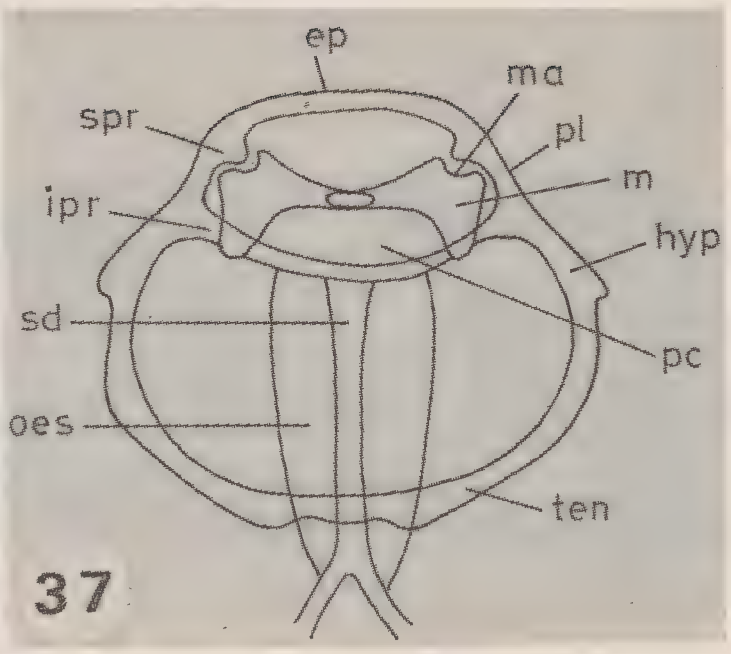
Prior to pupation, the larva expels several ovoid, dark brown meconia which line the walls of its cell inside the host, and turns translucent, whitish in color. This short prepupal stage is followed by a molt into the pupal stage.

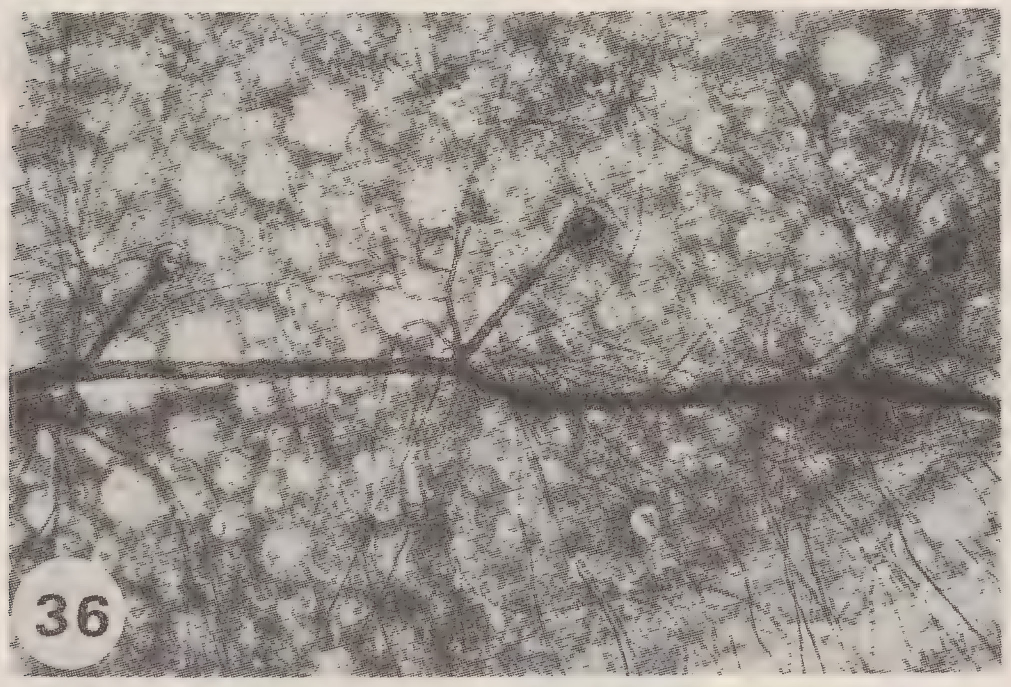
Pupa (Figs. 41-44): The newly-formed pupa is pale, translucent. It lies dorsal-side-up in its cell, surrounded by the meconia. In the female pupa,

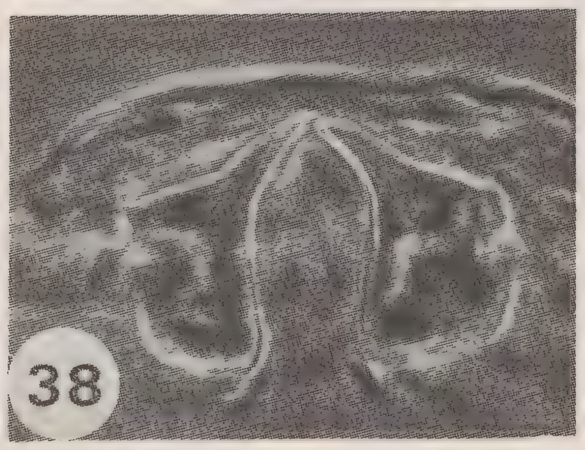


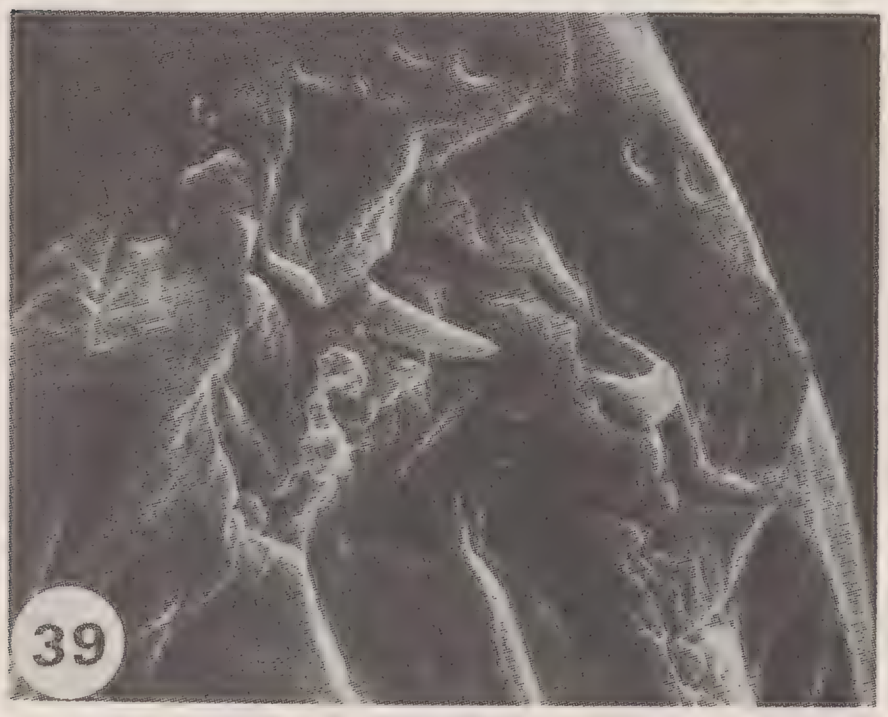
Figs. 28-34. **Diversinervus cervantesi** (Girault), developmental stages: 28, Ovarian egg. 29, Two eggs in host's gut. 30, Egg, 2 days old. 31, Egg, 4 days old. 32, First instar larva. 33, Mandibles of first instar larva. 34, Fully developed larva (SEM).

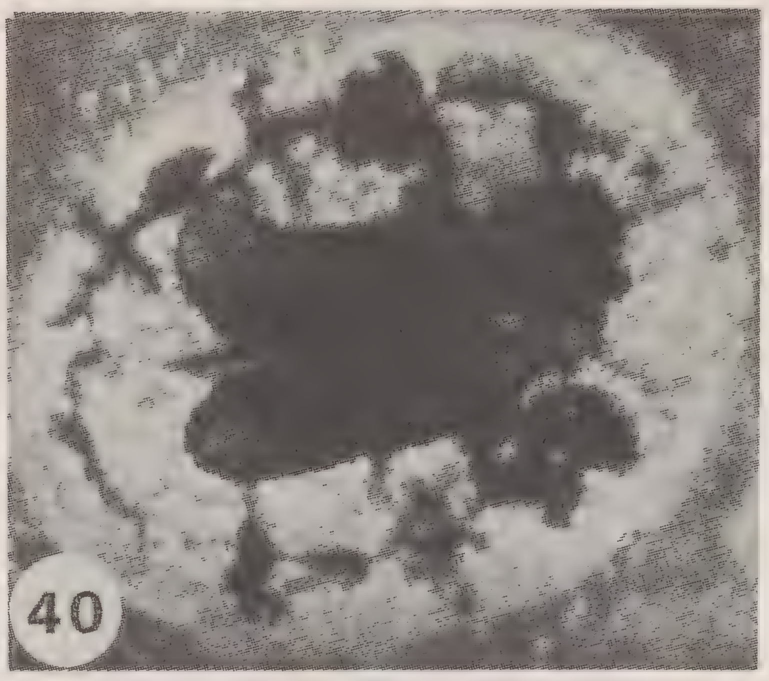




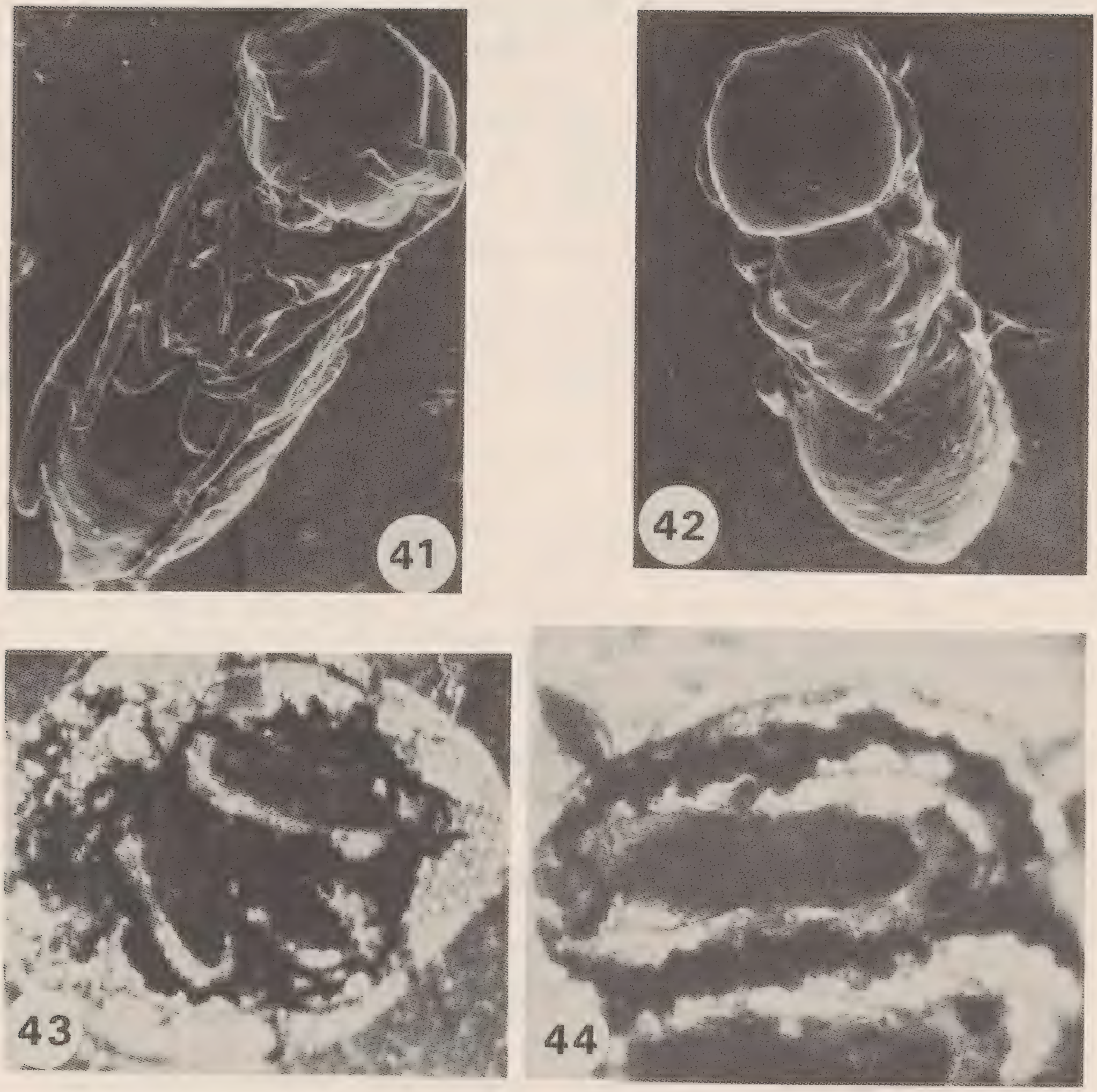








Figs. 35-40. **Diversinervus cervantesi** (Girault), developmental stages: 35,36, Respiratory system of fully developed larva. 37, Cephalic skeleton of fully developed larva (ep = epistoma; hyp = hypostoma; ipr = inferior pleurostomal ramus; m = mandible; ma = mandibular acron; oes = oesophagus; pc = preoral cavity; pl = pleurostoma; sd = salivary dut; spr = superior pleurostomal ramus; ten = tentorium; terminology adapted from Vance and Smith, 1933). 38, Mandibles of fully developed larva. 39, Cephalic region of fully developed larva, showing mandibles (SEM). 40, Two larvae in host.



Figs. 41-44. **Diversinervus cervantesi** : Developmental stages: 41, Female pupa, ventral view (SEM). 42, Female pupa, dorsal view (SEM). 43, Three female pupae in host. 44, Two male pupae in host.

pigmentation is first evident in a triangular area on the gaster, followed by the eyes, the mandibles and the rest of the body. In the male pupa, dark cross-bands first appear on the gaster, widening gradually and merging on the posterior segments, then anteriorly; the eyes become pigmented at about the same time; darkening of the thorax commences somewhat later, at the anterior end.

BIOLOGY

D. cervantesi is a primary, gregarious endoparasite of soft and wax scale insects (Homoptera: Coccidae). It was recorded in Australia from *Pulvinaria* sp. (Girault 1933), in Malaysia from the hemispherical scale, *Saissetia coffeae* (Walker), on coffee (Chua 1976). In Israel, it has been reared from the mesembryanthemum scale, *Pulvinaria mesembryanthemi* (Vallot), on *Mesembryanthemum edule*, from the hemispherical scale on coffee, from the Mediterranean black scale, *Saissetia oleae* (Olivier), on citrus and oleander, and from the Florida wax scale, *Ceroplastes floridensis* Comstock, on English ivy (Ben-Dov 1970, Kfir and Rosen 1980a, and in the present study). In the laboratory, we reared it successfully on the brown soft scale, *Coccus hesperidum* L., and that species served as host in all our biological studies.

Duration of Development at 28°C

Female wasps were allowed to oviposit for 24 hours in brown soft scales on a citron melon. The parasitized hosts were then kept in an incubator at 28°C, and a sample was dissected daily to determine the stage of development of the developing parasites.

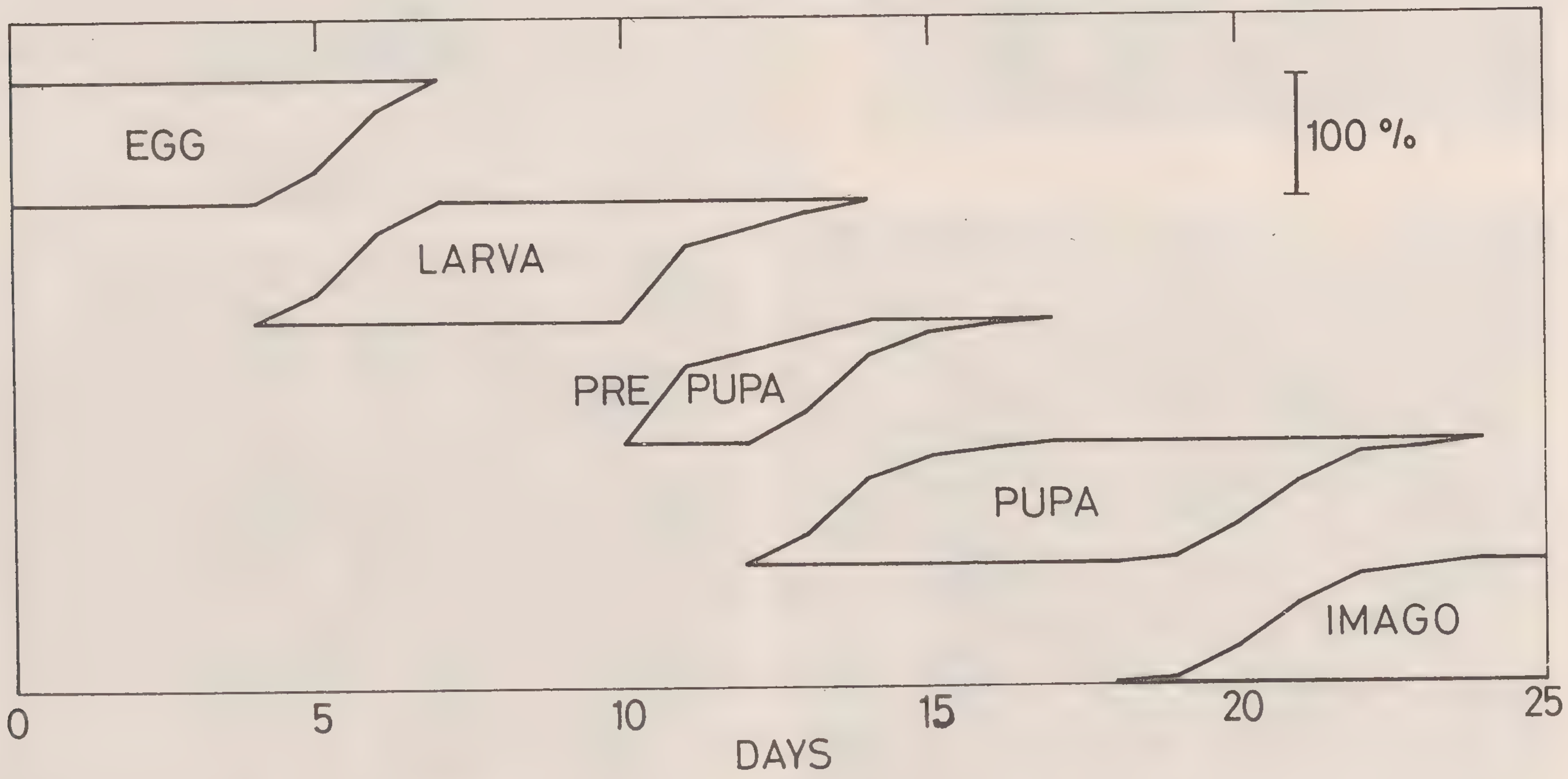


Fig. 45. **Diversinervus cervantesi:** Development of immature stages at 28°C.

The results are presented in Figure 45. Egg incubation was relatively long, about one-fourth of total development, the eggs hatching 5-6 days after deposition. Larval development took about one week, pupation occurring

12-15 days after oviposition. The pupal period was rather short, occupying only about one-third of the total; complete imaginal pigmentation was evident as early as on the 18th day, and emergence occurred 19-25 days after oviposition.

Effect of Temperature on Rate of Development

Female wasps were allowed to oviposit for 24 hours, and the citron melons bearing the parasitized hosts were then placed in incubators at constant temperatures of 20, 24, 28 and 32°C. Emergence of parasite progeny was recorded daily.

Table I. Duration of development of *D. cervantesi* F at constant temperatures.

Temperature (°C)	n	Duration of development (days)	
		Range	Average ± SD
20	664	39-50	43.84 ± 2.24
24	352	26-33	28.09 ± 1.49
28	1190	19-27	21.18 ± 1.30
32	0	-	-

As expected, the duration of development was progressively shorter at higher temperatures (Table I). No emergence occurred at 32°C. However, when hosts containing pupae of the parasite were exposed to 32°C, many of the parasites completed their development and emerged, indicating that this temperature is probably lethal mainly to the early developmental stages of *D. cervantesi*.

The equilateral hyperbola equation, based on the assumption that the product of developmental time and the corresponding temperature above a certain threshold is a constant (the *thermal constant*) for any given species, is a convenient way of expressing the effects of temperature on the duration of development of invertebrates (Bodenheimer 1926, 1958). The hyperbola equation for *D. cervantesi* was calculated as follows: Rates of development at 20, 24 and 28°C were obtained as the reciprocals of the actual developmental periods recorded at these temperatures; the linear regression ($y = a+bx$) of developmental rate on temperature was then calculated by the method of least squares; the parameters of the equilateral hyperbola (thermal constant, , and developmental threshold, c) were then obtained from the identities $ThC = 1/b$, $c = a/b$.

The regression of development rate on temperature and the corresponding equilateral hyperbola for *D. cervantesi* are presented in Figure 46. The developmental threshold was 12.47°C and the thermal constant 327.76 day-degrees.

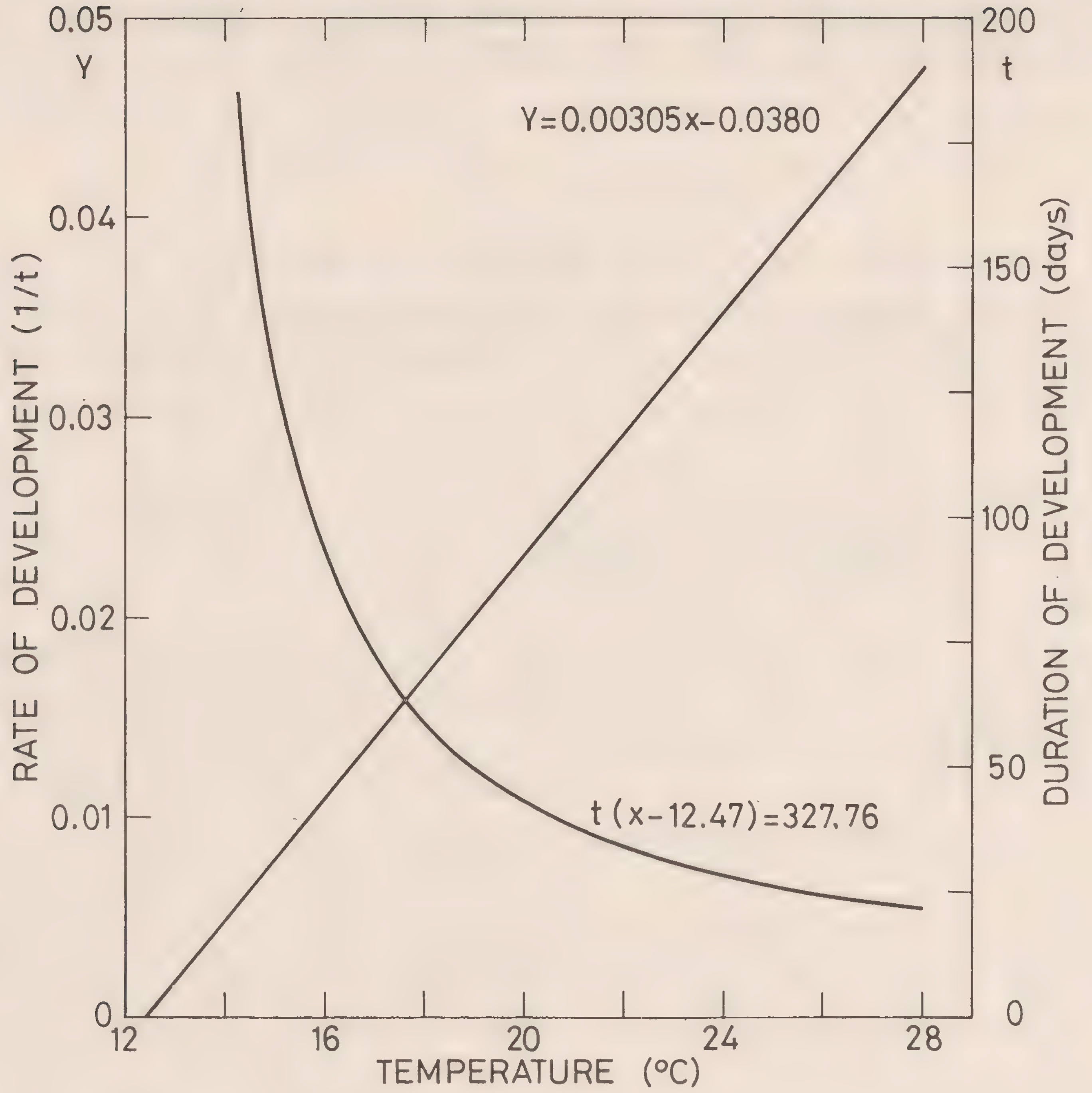


Fig. 46. **Diversinervus cervantesi:** Effect of temperature on rate and duration of development.

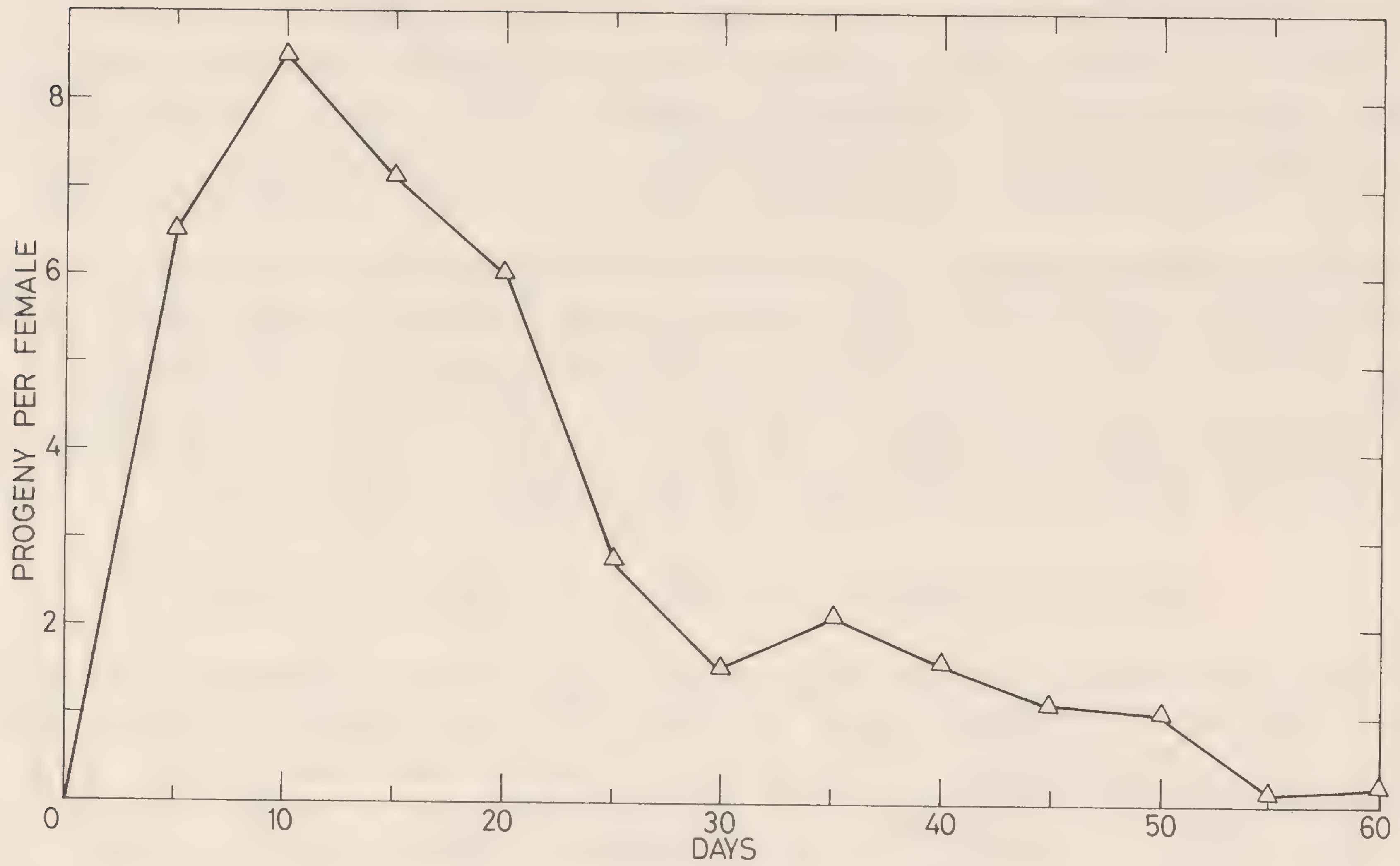
Reproduction and Fecundity

D. cervantesi is a deuterotokous species, unmated females usually giving rise to female progeny, occasionally to rare males. Of a total of 3278 specimens reared in the present study, 59, or 1.8 percent, were males.

Rearing temperatures in the range of 20-28°C did not affect the sex ratio even after several generations of continuous exposure. Some females exposed to 32°C during pupal development did not lay any eggs, whereas others started to do so only after 7 days at a lower temperature and they, too, produced the usual sex ratio.

Development is definitely gregarious. In the laboratory, only about 10 percent of the parasitized hosts examined yielded a single parasite, whereas about 50 percent yielded 4 parasites or more. Up to 13 parasites have been recorded from a single host. Several adults may emerge from one exit hole in the host's dorsum.

Similar data were obtained from dissection of parasitized hosts. Under normal conditions, practically all the eggs laid in a host develop to maturity. Only under extreme crowding did the number of eggs per host greatly exceed the number of emergent progeny, and dissection of such hosts indicated that



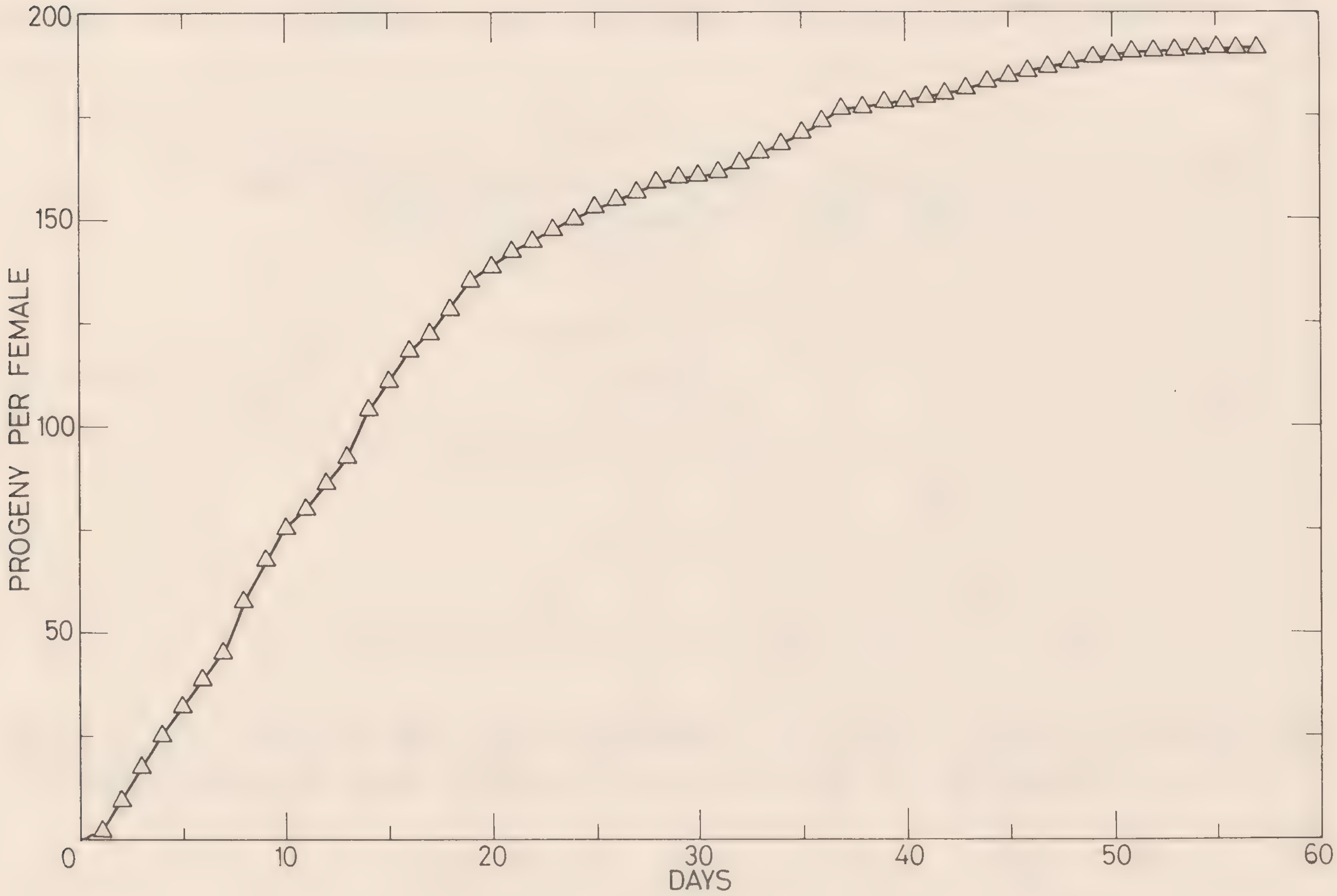


Fig. 47-48. **Diversinervus cervantesi:** 47, Daily fecundity (averages of 6 females). 48, Cumulative fecundity (averages of 6 females).

supernumerary parasites are eliminated in the egg or early larval stage. Progeny emergence was therefore used as the criterion for effective fedundity.

To assess the fecundity of *D. cervantesi*, 6 females were allowed to oviposit individually in brown soft scales on citron melons, at 26 ± 1°C and under constant illumination. (Preliminary observations had indicated that in darkness the fecundity is considerably lower). They were transferred daily to fresh hosts during the first week, every 1-3 days thereafter. Progeny emergence was recorded daily. The results are presented in Figures 47, 48.

The ovipositing females exhibited high longevity (20-67 days, average 45.5) and high fecundity (85-307 progeny per female, average 187). The species is synovigenic: Oviposition usually commenced on the seond day after emergence, or near the end of the first day, and continued throughout most of the female's adult life span. On the average, 72 percent of the progeny were produced during the first half of the female's adult life.

Effect of Relative Humidity on Adult Life Span

Freshly-emerged females of *D. cervantesi* were confined in clear plastic vials (diameter 43 mm, height 48 mm), the inner walls of which were smeared with a little honey. The mouth of each vial was covered with tissue paper and sealed with Permagum ® * to the mouth of a similar vial containing either dry P_2O_5 or a solution of 62.5 g KOH in 100 ml water, producing a relative humidity of 0 or 50 percent, respectively, in the sealed chambers thus formed (Peterson 1964). The vials were kept at 28°C, in the dark, and mortality of the wasps was recorded every few hours during the first two days, daily thereafter.

Table II. Longevity of adult *D. cervantesi* females at 0 and 50% relative humidity and 28°C.

RH (%)	n	Longevity (days)	Days to 50% mortality
0	44	1-4	1.5
50	40	2-42	17.0

The results (Table II, Fig. 49) indicate that the females of *D. cervantesi* are very sensitive to low relative humidity (see Bartlett 1962).

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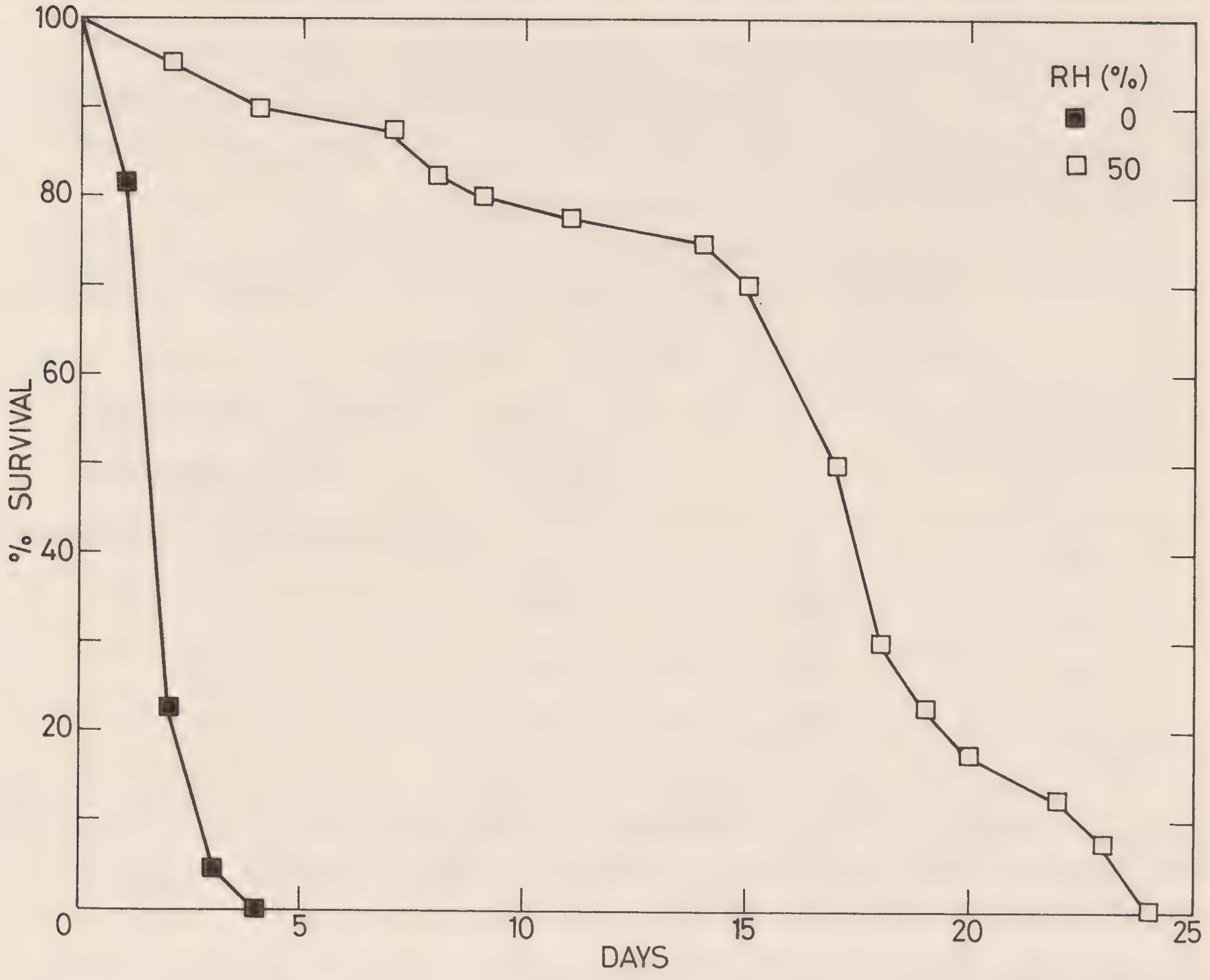
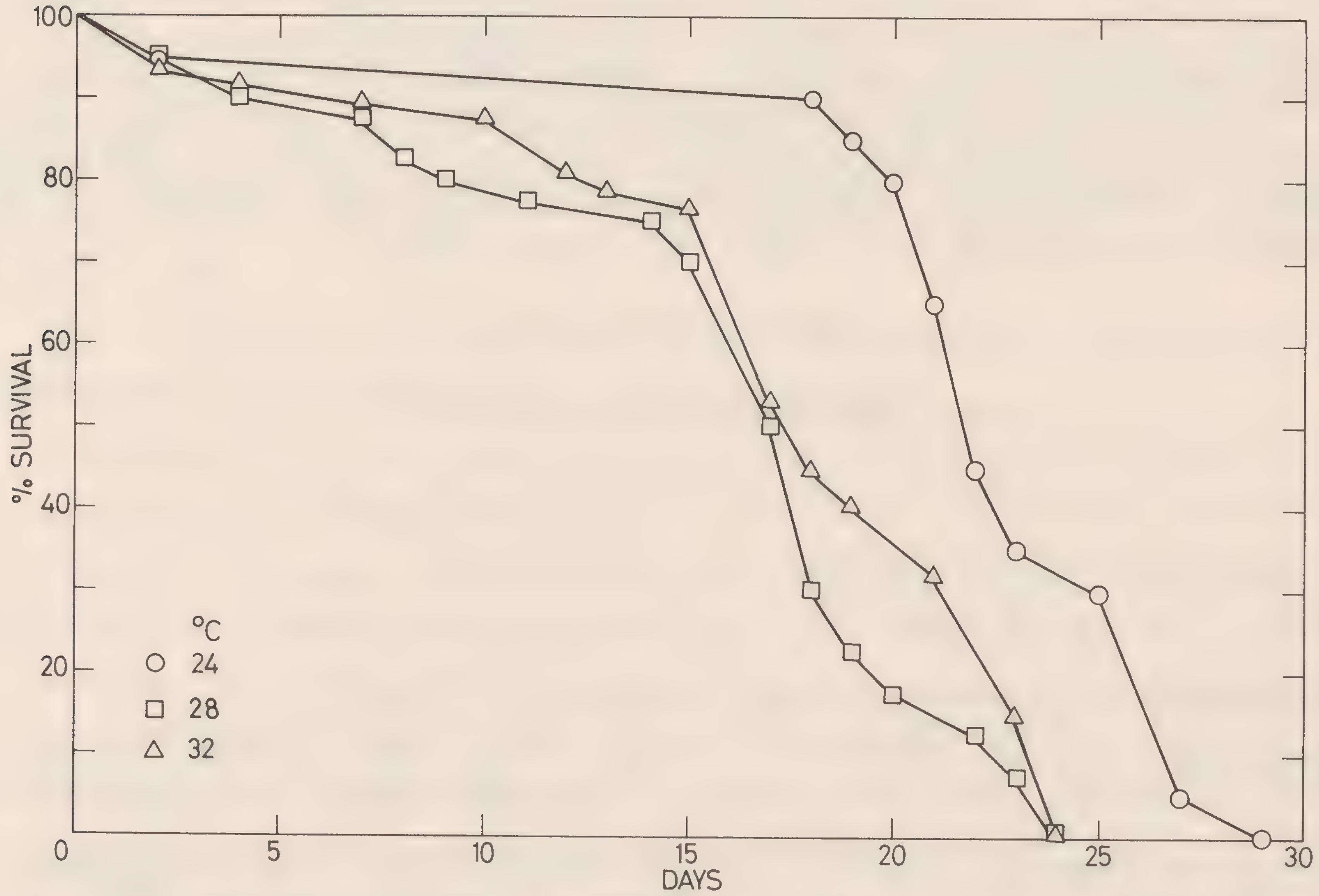
*A non-toxic, odorless sealing compound distributed by Virginia Chemicals, West Norfolk, VA.





Figs. 49-50. **Diversinervus cervantesi:** 49, Longivity of adult females at 0 and 50% RH and 28°C. 50, Longivity of adult females at various constant temperatures.

Effect of Temperature on Adult Life Span

Freshly-emerged females of *D. cervantesi* were confined in closed chambers, as described above, at 50 percent relative humidity with honey as food. The vials were kept at 24, 28 or 32°C, in the dark, and mortality of the wasps was recorded daily.

Table III. Longevity of adult *D. cervantesi* females at various constant temperatures.

Temperature (° C)	n	Longevity (days)	Days to 50% mortality
24	20	2-29	21.7
28	40	2-24	17.0
32	47	2-24	17.5

The results (Table III, Fig. 50) indicate that temperatures in the range of 24-32°C do not have a pronounced effect on the longevity of *D. cervantesi* females.

Although the wasps in this experiment were kept in the dark, which would presumably tend to reduce their activity and thus prolong their life span, even at 24°C their longevity in the absence of hosts was less than half that of the ovipositing females at 26°C and under constant illumination, as described earlier. This difference might be ascribed to predatory host-feeding which, however, was not observed in the present study, or to feeding on the honeydew produced by the hosts, etc. Similar observations have been reported for other coccid-inhabiting encyrtids (e.g., Kfir and Rosen 1980b).

SYNOPSIS OF THE SPECIES

Genus **DIVERSINERVUS** Silvestri

Diversinervus Silvestri (1915: 301-304). [Publ. Feb. 20, 1915].

Type-species: *Diversinervus elegans* Silvestri.

Cheiloneuroides Girault (1915: 96, 122). [Publ. June 4, 1915].

Type-species: *Cheiloneuroides bicristatus* Girault.

Taxonomy: Girault (1917: 37); Compere (1931: 233-235; 1938: 322-323; 1940: 407); Trjapitzin (1961: 671); Hayat *et al.* (1975: 39-41); Noyes (1980: 193).

The genus presently includes 10 valid species, which are listed below. An additional species, *D. intermedius* Hayat, Alam and Agarwal (1975: 43-44), described from a single female, ex *Chloropulvinaria psidii* (Maskell), India, has not been included here. From the description, it appears to be a small specimen of *D. elegans*.

Diversinervus cervantesi (Girault)

Cheiloneurus cervantesi Girault (1933: 4).

Distribution: Australia, Malaysia, Israel.

Hosts: Coccidae: *Ceroplastes floridensis* Comstock; *Coccus hesperidum* L. (in lab.); *Pulvinaria mesembryanthemi* (Vallot); *Pulvinaria* sp.; *Saissetia coffeae* (Walker); *S. oleae* (Olivier).

Diversinervus desantisi Compere

Diversinervus de santisi Compere (1931: 239-241).

Distribution: Eritrea.

Host: Coccidae: *Pulvinaria* sp.

Diversinervus elegans Silvestri

Diversinervus elegans Silvestri (1915: 304-305).

Cheiloneuroides bicristatus Girault (1915: 96-97).

Diversinervus meridionalis Compere (1931: 237-239).

Taxonomy: Girault (1917: 37); Compere (1931: 244-245; 1937: 43-44); Annecke (1964: 15); Rosen (1966: 61); Beardsley (1976: 189, 211).

Biology: Compere (1931); van den Bosch *et al.* (1955); Bartlett and Medved (1966); Rosen (1967); Bartlett (1978); Kfir and Rosen (1980a).

Distribution: Eritrea, Kenya, South Africa, Israel, Australia, Hawaii, Brazil, Peru, California (introd.).

Hosts: Coccidae: *Ceroplastes floridensis* Comstock; *Ceroplastes* sp.; *Coccus hesperidum* L., *C. pseudomagnoliarum* (Kuwana) (in lab.); *Gascardia brevicauda* (Hall); *G. destructor* (Newstead); *Marsipococcus proteae* (Brain); *Parasaissetia mangiferae* (Green); *Pulvinaria mesembryanthemi* (Vallot); *Saissetia coffeae* (Walker); *S. oleae* (Olivier); *S. persimilis* (Newstead); *Saissetia* spp.

For additional references see Peck (1963), Annecke and Insley (1971).

Diversinervus madgaoensis Hayat, Alam & Agarwal

Diversinervus madgaoensis Hayat, Alam and Agarwal (1975: 41-42, 44).

Distribution: India, Philippines.

Hosts: Coccidae: *Ceroplastes actiniformis* Green; *C. ceriferus* (Fabricius); *Pulvinaria* sp.

Note: Specimens of *D. madgaoensis* ex *C. ceriferus*, Banaras, India and ex *Pulvinaria* sp., Manila, Philippines, stand in the USNM.

Diversinervus masakaensis Compere

Diversinervus masakaensis Compere (1940: 407-408).

Distribution: Uganda.

Host: Coccidae: *Saissetia oleae* (Olivier).

Diversinervus paradisicus (Motschulsky)

Chiloneurus paradisicus Motschulsky (1863: 52).

Taxonomy: Compere (1931: 233-234); Trjapitzin (1961: 669-671).

Distribution: Sri Lanka.

Host: Coccidae: *Saissetia coffeae* (Walker).

Diversinervus scutatus Compere

Diversinervus scutatus Compere (1931: 235-237).

Distribution: South Africa.

Host: Coccidae: *Ceronema* sp.

Diversinervus silvestrii Waterston

Diversinervus silvestrii Waterston (1916: 137-140).

Distribution: Mauritius.

Host: Coccidae: *Coccus viridis* (Green).

Diversinervus smithi Compere

Diversinervus smithi Compere (1940: 408-410).

Biology: Flanders (1939, 1952).

Distribution: South Africa. Released in California but failed to become established (Bartlett 1978).

Host: Coccidae: *Saissetia oleae* (Olivier).

Diversinervus stramineus Compere

Diversinervus stramineus Compere (1938: 321-322).

Distribution: South Africa.

Host: *Saissetia persimilis* (Newstead).

SUBGENERIC CLASSIFICATION

The known members of *Diversinervus* seem to fall naturally into two species groups:

The elegans group: Female with tufts of bristles on both the mesoscutum and scutellum. In members with known males, the head of the male is dark metallic. Species in this group have banded eggs, and first-instar larvae with open tracheal systems. This group presently includes *desantisi*, *elegans*, *madgaoensis*, *paradisicus*, *scutatus*, *silvestrii* and *stramineus*.

The smithi group: Female lacking a tuft of bristles on the mesoscutum. In members with known males, the head of the male is yellow. Species in this group have unbanded eggs, and first-instar larvae with closed tracheal systems. This group presently includes *cervantesi*, *masakaensis* and *smithi*.

Although available information appears to support the establishment of these tentative groups, their validity and relationships are presently unclear.

For one thing, the males of *masakaensis*, *paradisicus* and *silvestrii* are still unknown, the male of *stramineus* was described without a head, and immature stages have not yet been described for most species. In the absence of a mesoscutar tuft as well as in immature characters, the **smithi** group appears to be more closely related to the genus *Cheiloneurus* than is the **elegans** group. On the other hand, however, *madgaoensis*, a member of the **eleans** group, resembles *Cheiloneurus* in having an elongate marginal vein in the female fore wing. For the time being, therefore, establishment of informal species groups appears preferable to formal classification into subgenera.

KEY TO THE SPECIES OF DIVERSINERVUS, FEMALES*

1. Mesoscutar tuft absent . . . . **The smithi group** 2
   Mesoscutar tuft present . . . . **The elegans group** 4

2. Frontovertex about one-fourth width of head, deeply emarginate posteriorly; antennal scape moderately expanded, clearly more than twice as long as wide; at least some funicular segments as long as wide, or longer; club shorter than the funicle and not much wider; ovipositor exserted somewhat; an arcuate, dark brown cross-band on face and cheeks 3
   Frontovertex wider, one-third width of head, not emarginate posteriorly; scape strongly expanded, twice as long as wide; all funicular segments wider than long; club large, as long as the funicle and considerably wider; ovipositor concealed; face and cheeks without a dark cross-band . . . . *masakaensis*

3. Wings greatly reduced; mesonotal and metanotal sclerites reduced, pronotum, tegulae and mesopleura relatively large; ocelli small, the posterior pair 5 times their own diameter from occipital margin; funicular segment V lined with dark brown dorsally; middle coxa dark brown . . . . *cervantesi*
   Wings fully developed; thoracic tergites normal; ocelli large, the posterior pair twice their own diameter from occipital margin; funicular segment V entirely yellow; middle coxa white . . . . *smithi*

4. Frontovertex densely reticulate-punctate, appearing granular 5
   Frontovertex smooth, shining, with tiny setigerous punctations 6

5. Scape strongly expanded, twice as long as wide; marginal vein of fore wing subequal in length to the stigmal vein; general coloration clay yellow . . . . *stramineus*
   Scape moderately expanded, more than twice as long as wide; marginal vein twice as long as the stigmal vein; general coloration dark metallic . . . . *madgaoensis*

6. Scape moderately expanded, more than twice as long as wide 7
   Scape strongly expanded, less than twice as long as wide; club large, nearly as long as the funicle; mesoscutar and scutellar tufts short, sparse . . . . *scutatus*

D. intermedius Hayat, Alam and Agarwal not included.

7. General coloration yellow; mesoscutum with a narrow metallic cross-band on posterior one-third 8

General coloration extensively metallic; mesoscutum golden to brownish-orange on either side of tuft, anterior part and sides black, with a wide metallic cross-band on posterior one-half; scape nearly 3 times as long as wide; club large, nearly as long as the funicle

8. Ocellar triangle acute; scape only a little more than twice as long as wide; club distinctly shorter than the funicle; gaster subequal in length to the thorax 9

Ocellar triangle right-angled; scape nearly 3 times as long as wide; club nearly as long as the funicle; gaster considerably shorter than the thorax . . . . *silvestrii*

9. Frontovertex very narrow, 6 times as long as wide, occupying one-ninth width of head; ovipositor exserted to one-eighth length of gaster; fore wing broad, twice as long as wide . . . . *paradisicus*

Frontovertex somewhat wider, about 4 times as long as wide, occupying one-sixth to one-fifth width of head; ovipositor exserted to one-fourteenth length of gaster; fore wing narrower, nearly 3 times as long as wide . . . . *elegans*

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